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## STUDIES IN THE HIPPOCASTANACEAE, IV. HYBRIDIZATION IN AESCULUS

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THE topic of hybridization is of prime importance in the study of the genus *Aesculus*, for much of the confusion concerning the concept of species and the problem of identification of the buckeyes in eastern North America has been due to the mongrel forms so often encountered in the natural populations and gardens. As early as 1869, Loudon stated:

“. . . the truth is, that the different kinds of *Aesculus* and *Pavia* cross-fecundate so freely, and seedlings vary so much, that there is no limit to the number of varieties that might be produced. The great error (because it creates so much confusion in the nomenclature) consists in giving these varieties to the world as species.”

Hybridization in the buckeyes involves only five of the fifteen species: *Aesculus hippocastanum*, and the four species of *Aesculus* section *Pavia* (*glabra*, *octandra*, *sylvatica* and *pavia*). *Aesculus parryi* of Baja California and *A. californica* of California are each geographically isolated and have not been found to hybridize, even under cultivation. *Aesculus parviflora* of Georgia and Alabama grows with *A. pavia* and *A. sylvatica* but does not hybridize with either. Its flowering period is two to four weeks later than either that of *A. pavia* or *A. sylvatica*, which apparently would serve as an effective seasonal or temporal isolation barrier. On the other hand, the fact that *A. parviflora* belongs to a different and distantly related section of the genus from *A. pavia* and *A. sylvatica* may explain the complete barrier to hybridization.

The only intersectional hybrid is *A. carnea* Hayne, which is an allopolyploid ( $n = 40$ ) resulting from the cross between *A. hippocastanum* and *A. pavia*. *Aesculus plantierensis* André is a sterile backcross ( $n = 30$ ) between *A. carnea* and *A. hippocastanum*. Both of these are garden hybrids and have been studied cytologically by Skovsted (1929) and Upcott (1936).

Many hybrids involving the sympatric species of section *Pavia* have been recognized, described, and given specific epithets. Both the hybrids arising under cultivation and the forms found in the natural populations will be discussed.

Many of the hybrids which have been given names represent forms which have arisen in various botanical gardens of Europe and America. Of the six possible hybrid combinations between the four species in section *Pavia*, all but two, *A. octandra*  $\times$  *sylvatica* and *A. glabra*  $\times$  *sylvatica*, have been previously described in the literature. The latter is still to be identified and there is no reason why it should not appear in cultivation.

Some hybrids involving three parental species have been given names. The exact crosses involved are unknown but it is possible occasionally to identify the parent species to which the hybrid is most nearly referable on the basis of all characteristics.

Johnson (1939) lists many of these cultivated hybrids, with short notes concerning their place of origin. It should be understood that in almost every case the parents of these hybrids have been determined from a study of comparative morphology. Although this is a sound criterion and there has been additional circumstantial evidence from the gardens as to the identity of the parents, none of the crosses was actually made experimentally. The significance of these hybrids arising under cultivation is that they match perfectly the putative hybrids found in the field, and therefore serve more or less as test crosses.

Since  $F_1$  hybrids are not commonly used in horticulture, and none forms a distinct population in nature, formulae instead of specific epithets are used in all cases. The binomials would become especially confusing since introgression is so prevalent, as indicated below.

Intermediate forms between species are often encountered in the field as well as in herbaria, and the interpretation of these intermediate forms is sometimes difficult. The major question

is just what the intermediate forms mean. They may be the result of introgression between distinct species, or an ancestral gene pool in which sympatric speciation is going on at the present time. Anderson (1953) has described a number of tests by which the distinction can be made between introgression and the gene pool hypothesis. The significant points in these five tests which indicate introgression are: 1) the loose association of variables characteristic of the variation pattern in artificially produced hybrids and backcrosses; 2) the introgressants found in the floristically newer or disturbed areas; 3) sterility, if any, showing up in the intermediates; 4) ability to predict, by the method of extrapolated correlates, the introgressing species; and 5) the similarity of experimental hybrids and backcrosses with the putative hybrids found in the field. In accordance with these five criteria, it is concluded that the intermediate forms found in *Aesculus* populations are the result of sympatric introgression. Much of the evidence in favor of this conclusion has been derived from the analysis of populations using the techniques developed by Anderson. Additional evidence is the high percentage of abortive pollen found in the intermediate forms, the similarity with hybrids arising in cultivation, and the prevalence of hybrids in disturbed habitats.

For an analysis of introgression in the buckeyes, I took random samples of twenty to fifty specimens each, from over thirty populations throughout the range of section *Pavia*. Each specimen consisted of a twig with a mature inflorescence and at least three or four leaves, and was selected from a mature part of the tree or shrub. In every case the entire population was briefly surveyed to obtain an idea of size and the habitat differences; following this the specimens were taken from along a transect through the population, and more or less equally spaced so that the specimens represented the entire length of the transect. Since the shrubby species are occasionally clonal by root sprouts, the spacing was necessary to eliminate the possibility of collecting more than one specimen from each clone.

The analysis of populations of "pure species," hybrid swarms, and those in which hybridization was suspected, was made by the use of pictorialized scatter diagrams as described by Anderson (1949, 1953). After determining the characters to use in this

analysis, the diagrams or graphs were plotted and grouped according to the species crosses. Each of these crosses will be discussed individually. The explanations of the symbols used for the characters are given with the diagrams.

During the preparation of the systematic treatment of the *Hippocastanaceae* in America, about 5000 herbarium specimens were examined and annotated. A word of explanation is in order concerning the method of annotating the hybrid forms. Since introgression is widespread in the populations of eastern United States, it is rare that a specimen taken from a wild population is exactly intermediate between two species, i. e., the  $F_1$  hybrid. Hybrids are more likely to represent backcrosses or various other recombinants. Usually such a backcross or recombinant can be referred to the parental species to which it is most nearly referable on the basis of all characters.

The specimens most nearly intermediate and which could not be placed with one or the other parent were annotated as "species A"  $\times$  "species B"—the names in alphabetical order. The backcrosses and recombinants were annotated as "species A" ( $\times$  "species B"), indicating that the specimen was most nearly referable to "species A" (which was probably the backcross parent), and that "species B" contributed the gene minority. There is some objection to this way of annotation, but as yet no other entirely satisfactory system has been proposed.

The citation of specimens is limited here to only one per county.

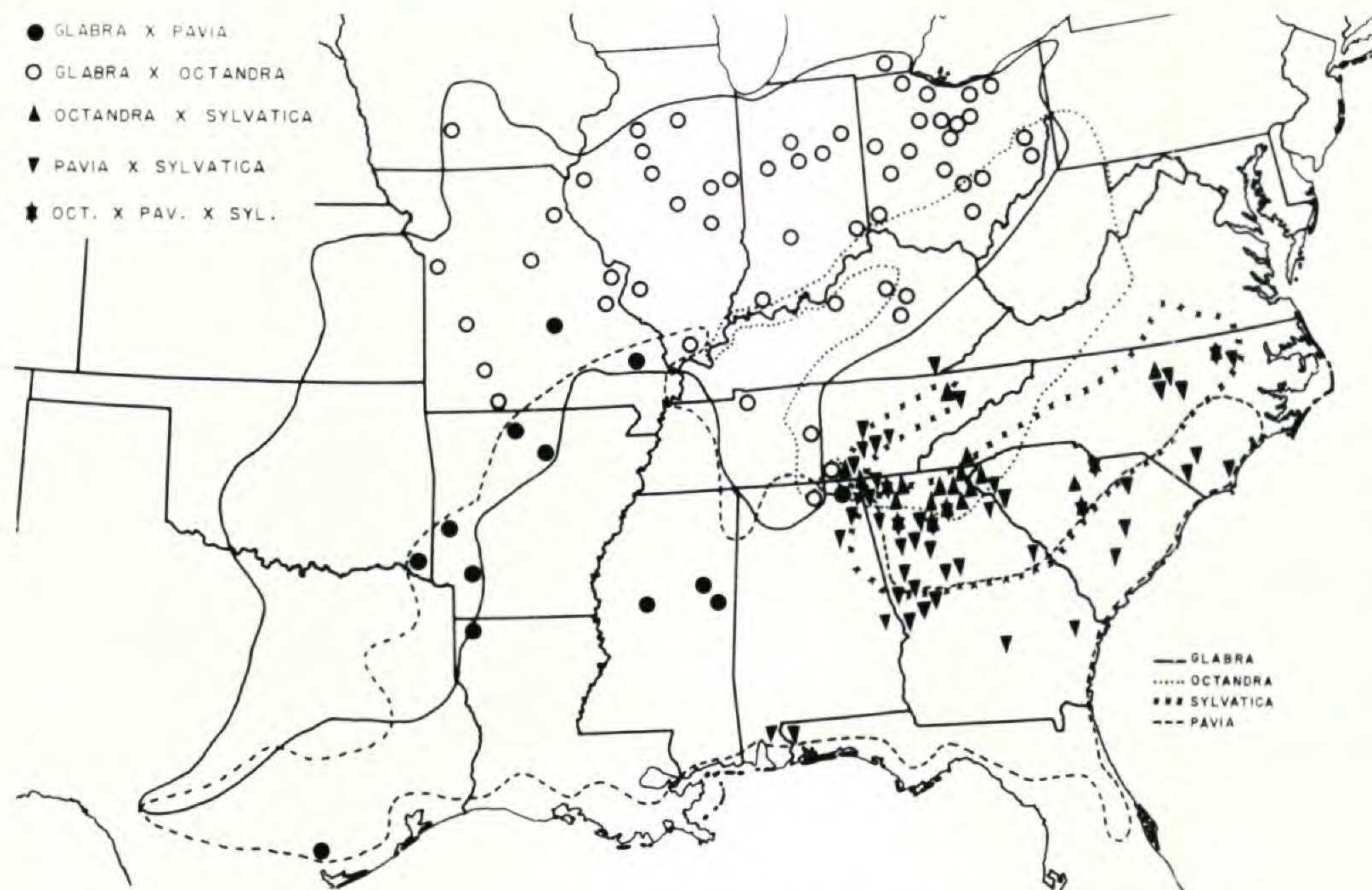
#### ***Aesculus glabra* $\times$ *octandra***

*Aesculus marylandica* Booth ex Kirchner, in Petzold and Kirchner, Arb. Muscov. 168. 1864.

*Aesculus glabra* forma *marylandica* Koehner ex Schelle, in Beissner et al., Handb. Laubh.-Ben. 322. 1903.

Intermediates between *A. glabra* and *A. octandra* may be recognized by their exserted stamens, stipitate glands on the pedicel and perianth surfaces, greater differences between upper and lateral petals than are found in *A. glabra*, and the irregularity of spines on the ovary wall.

A few  $F_1$  hybrids have been found; most of the intermediates, however, represent backcrosses or various recombinants. Since intermediates are detected by floral characteristics only, some



MAP 1. Distribution of hybrids in relation to the ranges of the species.

sterile specimens annotated and cited as *A. glabra* may actually be *A. glabra* (× *octandra*), which is very common north of the Ohio River, as shown in Map 1.

*Aesculus* × *arnoldiana* Sarg. (Jour. Arn. Arb. 5: 42. 1924.), occasionally cultivated in North America and Europe, represents a cross between *A. glabra* and the hybrid of *A. octandra* and *pavia*, or at least contains the characteristics of these three species, with *A. glabra* as the most apparent. According to Sargent this arose in the Arnold Arboretum about 1900.

One very interesting feature in the hybrids between *A. glabra* and *A. octandra* is the nature of the spines on the ovary wall. The effect of crossing a spiny-fruited type (*A. glabra*) with a smooth type (*A. octandra*) does not always result in the entire ovary being either spiny or smooth, or intermediate, but rather there is an unusual mosaic of spines on the wall—an irregularity which appears like sectorial chimeras in the pericarp. Particularly in the  $F_1$  hybrids, only one side on the immature ovary wall will have the stipitate glands (which develop into the spines on the pericarp), or one single row of glands from top to bottom, or a number of small glandular sections separated by smooth areas over the wall.

This "irregularity phenomenon" seems to occur when parents differ sharply in one or more characters. These characters will then be irregularly and asymmetrically expressed in the hybrid. Such irregularity has been described in a number of ferns (Wagner, 1954, 1956; Wagner and Hagenah, 1954).

**SPECIMENS EXAMINED.**—**Alabama:** Madison Co., 8 May 1881, *C. Mohr* (A).  
**Illinois:** Champaign Co., *F. C. Gates 1508.1* (MICH); Coles Co., *G. N. Jones 11143* (NY, UC); Hancock Co., 1 May 1844, *L. B. Mead* (MO, NY); Johnson Co., *E. J. Palmer 14971* (A, US); LaSalle Co., *J. W. Huett* (GH); Macon Co., *A. Gleason 281* (GH); Peoria Co., May 1890, *F. E. McDonald* (UC); St. Clair Co., 29 Apr. 1897, *H. Eggert* (NY); Stark Co., 15 May 1898, *Virginus H. Chase* (MO); Tazewell Co., May 1889, *McDonald* (GH); Vermilion Co., *Gates 1468* (US).  
**Indiana:** Cass Co., *C. C. Deam 19381* (A); Dearborn Co., *Deam 5691* (MO); Grant Co., *Hardin 673* (GA, MICH, NCSC); Howard Co., *R. C. Friesner 15066* (GH, MO, NY, UC); Monroe Co., *M. E. Springer 789* (GA, TEX); Tippecanoe Co., 3 May 1912, *L. O. Overholts* (MO); Warrick Co., *Deam 27087* (GH, NY); Wells Co., *Deam 758* (NY).  
**Iowa:** Madison Co., *Ada Hayden 7145* (MO).  
**Kentucky:** Bullitt Co., *P. A. Davies 249* (GH); Clark Co., *R. E. Horsey 1034* (A); Fayette Co., Apr. 1834, *R. Peter* (GH); Madison Co., *Horsey 1072* (A).  
**Michigan:** Lenawee Co., *Hardin 675* (GA, GH, MICH, NCSC).  
**Missouri:** Boone Co., *F. Drouet 1901* (GH); Greene Co., *Hardin 667* (GA, GH, MICH, NCSC); Marion Co., *J. Davis 1462* (A, UC); Jackson Co., *Bush 125* (A, GH, NY, US); Jefferson Co., 18 Apr. 1869, *Eggert* (NY, US); St. Clair Co., *Bush 13276* (A, MO); St. Louis Co., *Hardin 670* (GA, GH, MICH, NCSC); Taney Co., *Bush 4517* (A, MO).  
**Ohio:** Ashland Co., *Hardin 695* (GA, GH, MICH, NCSC); Belmont Co., *Hardin 690* (GA, GH, MICH, NCSC); Crawford Co., 14 May 1897, *Kellerman* (OS); Cuyahoga Co., May 1895, *G. B. Ashcraft* (NY); Fairfield Co., *Horsey 217* (A); Franklin Co., *Horsey 224* (A); Hamilton Co., *C. G. Lloyd 491* (MICH, US); Harrison Co., *Hardin 694* (GA, GH, MICH, NCSC); Logan Co., 9 May 1902, *Kellerman* (OS); Lorain Co., 21 May 1904, *F. O. Grover* (OS); Lucas Co., *Horsey 563* (A); Mercer Co., 12 May 1906, *S. E. Horlacher* (OS); Miami Co., 5 May 1883, *H. A. Young* (GH); Morrow Co., 20 Jul 1901, *Kellerman* (OS); Perry Co., Apr 1941, *F. Clean* (OS); Richland Co., *Horsey 475* (A); Sandusky Co., 2 Jun 1881, *R. P. Hayes* (OS); Vinton Co., 10 May 1901, *Kellerman* (OS); Wyandot Co., 10 May 1901, *T. A. Bonser* (OS).  
**Tennessee:** Franklin Co., 5 May 1898, *Eggert* (MO, NY); Rutherford Co., *Sharp et al. 11493* (TENN); Stewart Co., *A. W. Jobe 1823* (TENN).

The population in Vinton County, Ohio (Fig. 1) represents "pure" *A. octandra*, with the variation in size of flowers probably due to environmental conditions. The collections were made from large trees growing along a slope in a mixed mesophytic forest. Collections from Belmont County, Ohio, were taken from scattered trees and shrubs along a stream, through an open pasture, and to the edge of a beech-maple-buckeye woods, which had been lumbered recently. The population shown in Fig. 2 represents trees of *A. octandra*, with some influence from

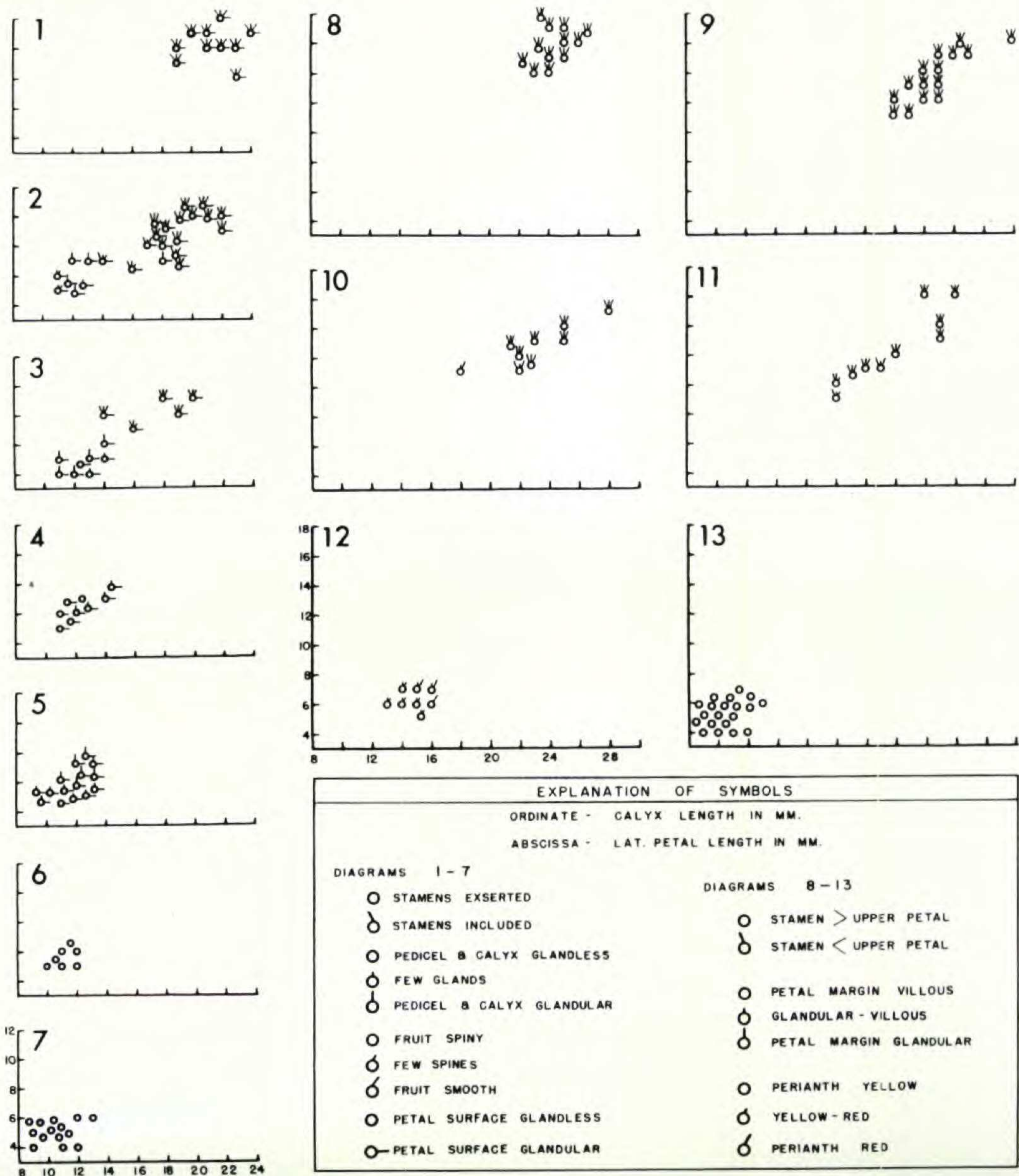


FIG. 1-7. Pictorialized scatter diagrams showing introgression between *A. glabra* and *A. octandra*. 1, *A. octandra* (Vinton Co., Ohio; Hardin 680). 2, *A. glabra* × *octandra* (Belmont Co., Ohio; H. 690, 691). 3, *A. glabra* × *octandra* (Belmont Co., Ohio; H. 692). 4, *A. glabra* (× *octandra*) (St. Louis Co., Mo.; H. 670). 5, *A. glabra* (× *octandra*) (Lenawee Co., Mich.; H. 675). 6, *A. glabra* (Guernsey Co., Ohio; H. 693). 7, *A. glabra* (Ark. and Mo.; H. 614, 616, 632, 639, 651). Fig. 8-13. Introgression between *glabra* and *A. pavia*. 8, *A. pavia* (Bowie Co., Texas; H. 570). 9, *A. pavia* (Tallahatchie Co., Miss.; H. 109). 10, *A. pavia* (× *glabra*) (Holmes Co., Miss.; H. 466). 11, *A. pavia* (× *glabra*) (Bossier Par., La.; H. 507). 12, *A. glabra* (× *pavia*) (Polk Co., Ark.; H. 598). 13, *A. glabra* (Ark. and Mo.; H. 597, 614, 616, 632, 639, 651).

*A. glabra*, and then shrubs along the creek which are *A. glabra* with introgression from *A. octandra*. Figure 3 is similar and represents a population in which *A. octandra* was found on the

ridges and *A. glabra* in the valley along a stream. The hybrids were scattered throughout the entire area, which had been cut over and was partly under cultivation and pasture.

The populations shown in Fig. 4 and 5 are typical of many scattered throughout Ohio, Kentucky, Indiana, Illinois, Missouri, and into Iowa (Map 1). In these, the specimens are referred to *A. glabra*, but they indicate, by the presence of stipitate glands, the influence of *A. octandra*. Figure 6 and 7 represent populations of "pure" *A. glabra* from Ohio and Arkansas. The smaller sized flowers in Arkansas are typical of the western populations, and the wide variation shown by Fig. 7 is because the specimens are from a number of different small populations in the region rather than a single local population.

It is evident from the diagrams that hybrids which are most nearly intermediate occur in the zone of overlap between the two species. In these areas there is some degree of reciprocal introgression. On the other hand, northward and westward in glaciated areas where *A. octandra* does not exist, there has been a widespread infiltration of some germplasm of *A. octandra* into the populations of *A. glabra*.

#### ***Aesculus glabra* × *pavia***

*Aesculus* × *bushii* Schneider, Ill. Handb. Laubh. 2: 251. 1912.

*Aesculus* × *mississippiensis* Sarg., Jour. Arn. Arb. 2: 120. 1920.

Hybrids between *A. glabra* and *A. pavia* may be recognized by the flower color (yellow-red), stamens usually exserted, petals unequal, petal margin and surface glandular-pubescent, and pericarp irregularly spiny.

Intermediate forms due to hybridization are found, although infrequently, mostly in the region of overlap between ranges of the two parental species (Map 1), in northern Alabama, east-central Mississippi, Louisiana, southeastern Texas (*A. glabra* var. *arguta* × *pavia*), Arkansas, southeastern Oklahoma and eastern Missouri. There are outlying stations for *A. glabra* in east-central Mississippi which account for the presence of hybrids in this region.

**SPECIMENS EXAMINED.**—**Alabama:** Jackson Co., *Harbison 1061* (NCU). **Arkansas:** Hempstead Co., *Bush 1098* (A); Marion Co., *D. M. Moore 516* (UARK); Polk Co., *Hardin 598* (CA, GH, MICH, NCSC); Stone Co., 26 Apr 1928,



*Ashe* (NCU). **Louisiana:** Bossier Par., *Hardin 507* (GA, GH, MICH, NCSC). **Mississippi:** Holmes Co., *Hardin 466* (GA, GH, MICH, NCSC); Noxubee Co., *Harbison 1061* (A, NCU); Oktibbeha Co., *Harbison 1055* (A). **Missouri:** Bollinger Co., *Steyermark 28404* (NY, US); Phelps Co., *B. H. Slavin 235* (A). **Oklahoma:** McCurtain Co., 14 Apr 1940, *C. G. Ward* (GA). **Texas:** Jackson Co., *S. G. Drushel 10512* (A).

Analyses of populations showing introgression between *A. glabra* and *A. pavia* are illustrated in Figs. 8–13. Reciprocal introgression between these two species is apparently restricted, for there is very little detectable influence on either parental species away from the area of the original crosses (Map 1). Figures 8 and 9 indicate populations of *A. pavia* in Texas and Mississippi. The Mississippi population (Fig. 9) is variable with respect to flower size, probably due to ecological conditions. The plants were growing in mixed hardwoods on the steep slopes of the loess hills and were under varying light conditions. The two populations shown in Figs. 10 and 11 are considered as *A. pavia*, but with slight introgression from *A. glabra* evidenced by the variation in color and glandular condition of the perianth. Both populations were in disturbed areas along county roads, and on the Coastal Plain which is the typical habitat for *A. pavia*.

In Polk County, Arkansas, and on the edge of Big Fork Creek just east of the town of Big Fork, there were a few trees which looked like *A. glabra*, but the flowers were reddish and had a few glands on the petal margins (Fig. 12). These show practically no variation among themselves, and may possibly represent a number of F<sub>1</sub> hybrids or backcrosses with *A. glabra*. *Aesculus glabra* was common throughout the area and along the creek; no *A. pavia* was found in the region. To give an indication of *A. glabra* in this series of scatter diagrams, populations from Arkansas have been graphed in Fig. 13.

#### ***Aesculus octandra* × *sylvatica***

*Aesculus glaucescens* Sarg., *Trees and Shrubs* 2: 257. 1913; in part and as to type.

The hybrid forms between *A. octandra* and *A. sylvatica* may be recognized mainly by their shrubby or small tree habit and the few stipitate glands mixed with tomentum on the pedicel and/or the lower part of the calyx. The result of introgression has been primarily an increased variation in the populations of *A. sylvatica*, although some reciprocal introgression takes place.

The type specimen for *A. glaucescens* is Harbison's no. 619, collected May 18, 1911 in Banks County, Georgia (A). This population (Harbison nos. 610, 618, 619, and 620) appears as a hybrid swarm between *A. octandra* and *A. sylvatica*, these collections and the duplicates of 619 representing different recombinants or the parent trees of *A. octandra*. From Sargent's description, *A. glaucescens* would be a synonym of *A. sylvatica* as defined by me, but the type specimen happens to be one of the recombinants belonging under this hybrid designation.

The hybrid forms between these two species are mostly found in the region of overlap between the parental species, in southeastern Tennessee, western North Carolina, northern Georgia, and northwestern South Carolina (Map 1).

**SPECIMENS EXAMINED.**—**Georgia:** Banks Co., *Duncan & Hardin 16304* (GA); Dade Co., *Duncan 2417* (GA); Dawson Co., *Duncan & Adams 18536* (GA, MICH); Gordon Co., *Duncan 2507* (UC); Habersham Co., *Harbison 1576* (A, NCU); Hall Co., 8 May 1926, *Ashe* (A, NY); Lumpkin Co., *Duncan & Hardin 16007* (GA); Murray Co., *Duncan 15770* (GA); Rabun Co., *Harbison 23* (A); Stephens Co., *Harbison 6* (A). **North Carolina:** Macon Co., *Harbison 11* (A); Orange Co., Apr 1896, *Ashe* (NCU). **South Carolina:** Fairfield Co., *Hardin 112* (GA, MICH, NCSC); Lancaster Co., *Duncan & Hardin 15610* (NCU); Oconee Co., *McVaugh 5658* (A, UC). **Tennessee:** Franklin Co., *P. H. Webb 180* (TENN); Grainger Co., 13 May 1945, *S. A. Cain* (TENN).

Populations of *A. sylvatica* are shown in Figs. 27–30; all show relatively little variation. They are found in generally undisturbed mixed hardwoods and under fairly uniform environmental conditions. The populations in Figs. 32 and 33 are *A. sylvatica* with a strong influence from *A. octandra*, and *A. octandra* with influence from *A. sylvatica*, respectively. The two populations were found in mixed hardwoods which had been cut over to some extent. The typical *A. octandra*, from western North Carolina, is seen in Fig. 34.

#### ***Aesculus pavia* × *sylvatica***

*Pavia mutabilis* Spach, Ann. des Sci. Nat., Bot., Sér. 2, 2: 57. 1834.

*Aesculus mutabilis* (Spach) Schelle, in Beissner et al., Handb. Laubh.-Ben. 323. 1903.

*Aesculus* × *harbisonii* Sarg., Trees and Shrubs 2: 259. 1913.

*Aesculus* × *mutabilis* var. *penduliflora* Sarg., Jour. Arn. Arb. 5: 48. 1924.

*Aesculus* × *mutabilis* var. *induta* Sarg., l. c. 48. 1924.

*Aesculus* × *mutabilis* var. *harbisonii* (Sarg.) Rehd., Jour. Arn. Arb. 7: 241. 1926.

Hybrid forms between *A. pavia* and *A. sylvatica* may usually be recognized by flower color (yellow-red) and petal margins glandular-villous.

The F<sub>1</sub> hybrids, backcrosses and recombinants are rather common in the Piedmont and Coastal Plain of the Carolinas, Georgia and Alabama, and also northward in the Ridge and Valley Province of eastern Tennessee into southern Kentucky (Map 1). Some well known populations, e. g., around Lea Lakes in Grainger County, Tennessee, Sequatchie Valley of Tennessee (Svenson, 1941), and Stone Mountain, Georgia (Hardin, 1957), have been favorite collecting areas for many years and are now recognized as hybrid swarms. The Stone Mountain population is of particular interest since it is the type locality for a number of species and varieties.

Hybrids between *A. pavia* and *A. sylvatica* were found as early as the middle 1800's in European gardens. Many of the names listed here in synonymy were based on the hybrids which arose in cultivation, or the seeds were collected in the field and planted in the Arnold Arboretum. The various varieties of *A. × mutabilis* described by Sargent represent different backcrosses or recombinants and later segregates which arose under cultivation.

**SPECIMENS EXAMINED.**—**Alabama:** Baldwin Co., *J. G. Jack 2979* (US); DeKalb Co., *Harbison 555* (A); Etowah Co., *Harbison 543* (A, MO); Lee Co., *Duncan 9174* (GA, MO). **Florida:** Escambia Co., *Harbison 4128* (NCU); Liberty Co., yr. 1868, *B. F. Saurman* (PG). **Georgia:** Bartow Co., *Duncan 8028* (GA, GH, TENN, UC, US); Bryan Co., *Pryon & McVaugh 1384* (GA); Butts Co., *Hardin 104* (GA, MICH, NCSC); Catoosa Co., *Duncan 15764* (GA); Chatooga Co., *Duncan & Hardin 15919* (GA, MICH); Cobb Co., *Duncan 13489* (GA); Coweta Co., *Duncan & Huttleston 10707* (GA); Crawford Co., *Hardin 101* (GA, MICH, NCSC); DeKalb Co., *Hardin 107* (GA, MICH, NCSC); Floyd Co., *Duncan & Hardin 15252* (GA, MICH); Forsyth Co., *Duncan 5268* (GA); Fulton Co., *Duncan 9347* (GA); Hall Co., *Duncan 18569* (GA); Hart Co., *Duncan 4825* (GA, GH, MO, UC, US); Jasper Co., Apr 1842, *T. C. Porter* (GH); Meriwether Co., *Duncan & Huttleston 10765* (GA); Muscogee Co., 14 Apr 1940, *L. R. Kische* (NCU); Paulding Co., *Pryon & McVaugh 2599* (GA); Richmond Co., 18 Mar 1909, *C. S. Sargent* (A); Talbot Co., 7 Aug 1941, *O. Battle* (US); Telfair Co., 9 Apr 1918, *Harbison* (NCU); Troup Co., *Duncan & Huttleston 10793* (GA); Upson Co., *A. Cronquist 4337* (GA, GH, MO, US); Whitfield Co., *Duncan 15769* (GA). **Kentucky:** Bell Co., *H. A. Gleason 8831* (NY); "southern Ky.", May-Aug 1900, *Sadie F. Price 2385* (GH). **North Carolina:** Bladen Co., *Radford 6871* (NCU); Columbus Co., *C. V. Morton 2122* (US); Durham Co., *Harbison 15100* (NCU); Halifax Co., Apr 1894, *C. S. Williamson* (PH); New Hanover Co., May 1867, *W. M. Canby* (MICH, PH); Orange Co., 2 May 1916, *H. R. Totten* (NCU); Wake Co., *Harbison 7* (A). **South Carolina:** Anderson Co., yr. 1886, *F. H. Earle*

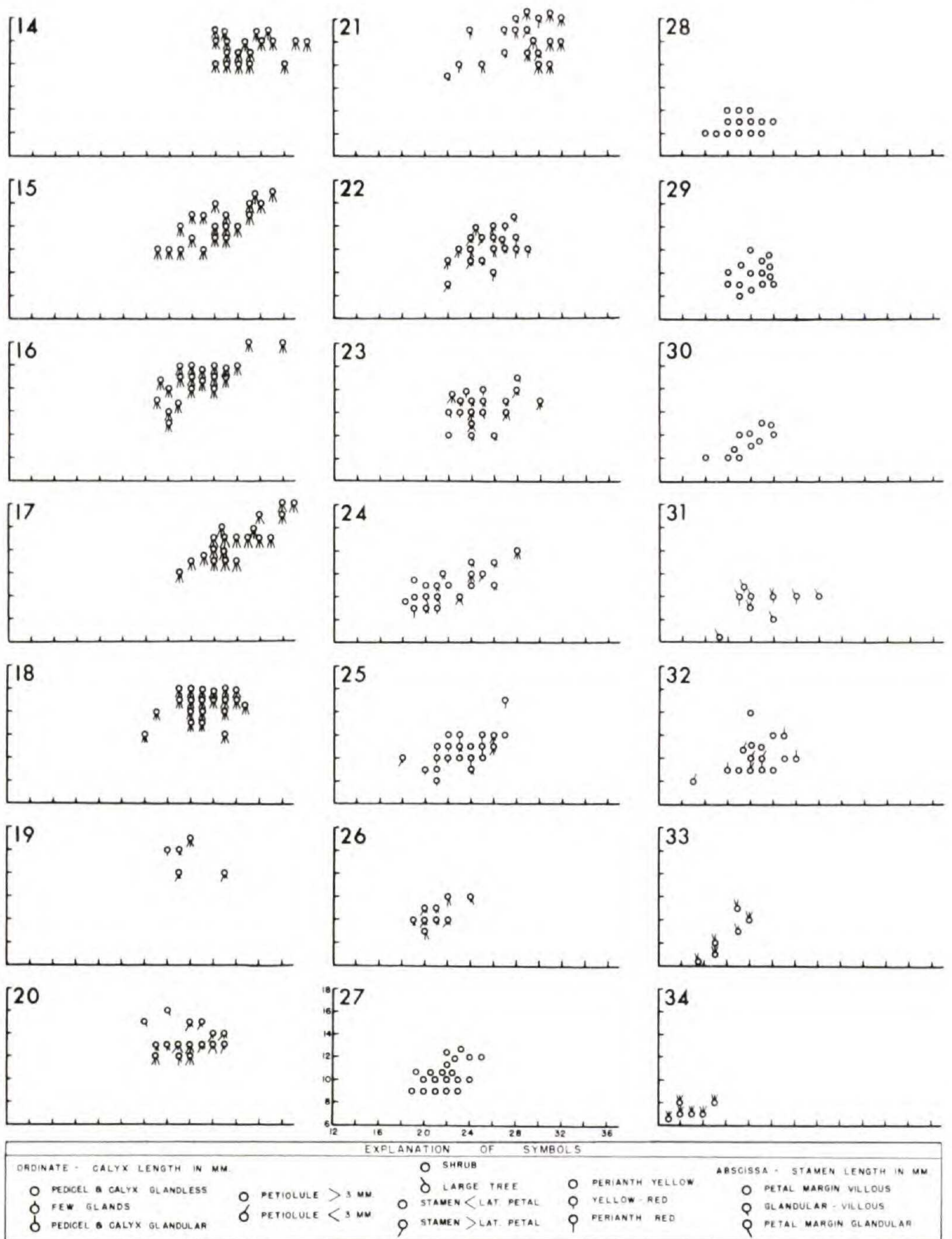


FIG. 14-34. Pictorialized scatter diagrams showing introgression between *A. pavia*, *sylvatica* and *A. octandra*. 14, *A. pavia* (Appling Co., Ga.; H. 105). 15, *A. pavia* (Geneva Co., Ala.; H. 102). 16, *A. pavia* (Crenshaw Co., Ala.; H. 103). 17, *A. pavia* (Effingham Co., Ga.; H. 106). 18, *A. pavia* (Winston Co., Ala.; H. 108). 19, *A. pavia* ( $\times$  *sylvatica*) (Catoosa Co., Ga.; Duncan 12350). 20, *A. pavia* ( $\times$  *sylvatica*) (Floyd Co., Ga.; Duncan 15750). 21, *A. pavia* ( $\times$  *sylvatica*) (Crawford Co., Ga.; H. 101). 22, *A. pavia*  $\times$  *sylvatica* (DeKalb Co., Ga.; H. 129). 23, *A. pavia*  $\times$  *sylvatica* (DeKalb Co., Ga.; H. 107). 24, *A. sylvatica* ( $\times$  *pavia*) (Butts Co., Ga.; H. 104). 25, *A. sylvatica* ( $\times$  *pavia*) (Hart Co., Ga.; H. 111). 26, *A. sylvatica* ( $\times$  *pavia*) (Troup Co., Ga.; Duncan 10793). 27, *A. sylvatica* (Morgan Co., Ga.; Duncan 10825). 28, *A. sylvatica* (Union Co., S. C.; H. 113). 29, *A. sylvatica* (Clarke

(NY); Clarendon Co., *W. Stone 624* (PH); Darlington Co., *B. E. Smith 1615* (NCU); Dorchester Co., *Duncan 5902* (GA); Oconee Co., *Harbison 6* (A). **Tennessee:** Bledsoe Co., *Shanks 1390* (TENN); Grainger Co., *M. Webster 28* (GA); Marion Co., *Shanks, Hardin, Woods & Barkley 15464* (TENN); Rhea Co., *Sharp 19071* (TENN); Sequatchie Co., *Cain & Sharp 4398* (NY, TENN); Van Buren Co., 27 Apr 1952, *J. E. Byrd* (TENN).

The populations of "good" *A. pavia* are shown in Figs. 14–18. There is some variation, in size of flowers, between populations and within single populations which is probably due to ecological conditions. Each of these populations was found in a relatively mature area under mixed hardwoods and in well-drained soils.

The populations shown in Figs. 19–21 represent *A. pavia* with influence from *A. sylvatica*. Figures 22 and 23 are the populations from Stone Mountain, Georgia, which have been previously described (Hardin, 1957). The populations in Figs. 24–26 are primarily *A. sylvatica* with strong influence from *A. pavia*. These intermediate populations for the most part were found in disturbed areas, along road sides, heavily lumbered woods, pastured lands, or the edges of cultivated farms. *Aesculus sylvatica* is represented in Figs. 27–30.

The reciprocal introgression between these two species has resulted in a heightened variability in the two parental species, and this gene flow has gone far into the populations of the parental species and away from the region of the original crosses (Map 1).

#### ***Aesculus octandra* × (*pavia* × *sylvatica*)**

*Aesculus woerlitzensis* Koehne, Repert. Sp. Nov. Reg. Veg. **11**: 396. 1913.

*Aesculus woerlitzensis* var. *ellwangeri* Rehd., Mitt. Deutsch. Dendr. Ges. 1913 (22): 258. 1914.

*Aesculus* × *dupontii* Sarg., Jour. Arn. Arb. **5**: 46. 1924.

*Aesculus* × *dupontii* var. *hessei* Sarg., l. c. 47. 1924.

Occasional specimens have been seen which have characters of the three species *A. octandra*, *A. pavia* and *A. sylvatica*. Most of these are best represented (at least on the basis of morphological characteristics) as *A. octandra* × (*pavia* × *sylvatica*) and recognized by glandular-villous petal margins, yellow-red flowers, and with stipitate glands mixed with tomentum on the

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Co., Ga.; H. 117). 30, *A. sylvatica* (Elbert Co., Ga.; H. 116). 31, *A. sylvatica* × *octandra* × *pavia* (Gordon Co., Ga.; Duncan 15744). 32, *A. sylvatica* (× *octandra*) (Fairfield Co., S. C.; H. 112). 33, *A. octandra* (× *sylvatica*) (Murray Co., Ga.; Duncan 15770). 34, *A. octandra* (Ga., N. C., Tenn.; H. 118–122, 131, 725).

pedicels and lower part of the calyx. These hybrids are not very different from the *A. octandra* × *pavia*, but the petal margins are more like the *A. pavia* × *sylvatica* hybrid.

The specimens labeled as *A.* × *dupontii* and grown at the Arnold Arboretum and at the Botanical Gardens, University of Michigan (from the type tree in front of the DuPont mansion, Winterthur, Delaware), show characteristics of all three of these species. Just what the original crosses were, of course, is not known. Sargent, in the original description, supposed that the cross was between *A. pavia* and *A. sylvatica*, but he overlooked the important glands on the pedicels—a characteristic only of *A. octandra*.

*Aesculus woerlitzensis*, and its variety, originated in European gardens or nurseries—the actual origin is unknown. They have been cultivated in the Arnold Arboretum and other gardens in the United States for many years.

Since *A. sylvatica* is located in the relatively narrow Piedmont between *A. octandra* of the Appalachians and *A. pavia* of the Coastal Plain, and since the apparent gene flow from these two species extends some distance into *A. sylvatica* from the areas of original hybridization, occasional populations of *A. sylvatica* would be expected to show influence from both *A. pavia* and *A. octandra*. Such populations with various degrees of influence from the three parental species have been found (Map 1). The population in Gordon County, Georgia, is shown in Fig. 31.

**SPECIMENS EXAMINED.**—**Georgia:** Bartow Co., *Duncan 8094* (GA); Forsyth Co., *Duncan 5268* (GA); Gordon Co., *Duncan 15744* (GA); Hall Co., *Duncan 18569* (GA, MICH); Whitfield Co., *Duncan 15769* (GA). **North Carolina:** Halifax Co., 27 Apr 1897, *J. K. Small* (NY). **South Carolina:** Lancaster Co., *Duncan & Hardin 15610* (GA, NCU); Richland Co., 13 Apr 1937, *J. H. Chapman* (GA).

#### ***Aesculus octandra* × *pavia***

- Aesculus hybrida* DC., Cat. Hort. Monsp. 75. 1813.  
*Pavia hybrida* (DC.) DC., Prod. 1: 598. 1824.  
*Aesculus pavia* var. *arguta* Lindl., Bot. Reg. 993. 1826.  
*Pavia livida* Spach, Ann. des Sci. Nat., Bot., Sér. 2, 2: 56. 1834.  
*Pavia hybrida* Spach, l. c. 57. 1834.  
*Pavia versicolor* Spach, l. c. 57. 1834.  
*Pavia lindleyana* Spach, l. c. 59. 1834.  
*Pavia arguta* (Lindl.) Raf., Alsog. Am. 74. 1838.  
*Aesculus versicolor* Wenderoth, Ind. Sem. Hort. Acad. Marburg. 1853: 4. 1853.

*Aesculus flava* var. *purpurascens* Gray, Man. Bot. N. U. S., ed. 2, 83. 1856.

*Aesculus octandra* var. *hybrida* Sarg., Silva No. Amer. 2: 60. 1891.

*Aesculus octandra* var. *purpurascens* (Gray) Schneider, Ill. Handb. Laubh. 2: 252. 1912.

This hybrid is recognized by flower color (red-yellow), the stipitate glands on the pedicel and glandular-pubescent petal margin.

No natural hybrids between these two species have been recognized. Garden hybrids, however, representing this cross have long been in cultivation. Sargent (1913) states that *A. hybrida* appeared in the Botanic Garden at Montpellier early in the nineteenth century. It is now cultivated in many varieties in Europe and to a lesser extent in America.

Early records of *A. hybrida* (or synonym) from West Virginia, Virginia and Maryland are probably based on the cultivated hybrids of European origin. Sargent (1913) presents a clear account of the history of these hybrids and the confusion which they have brought about in the nomenclature of the natural populations in eastern America.

With sympatric introgression occurring in these species of section *Pavia*, the identity of the entities is maintained by ecological and/or internal barriers of various kinds. The effectiveness or strength of these barriers (whatever they may be) varies among the different crosses. For example, introgression between *A. glabra* and *A. pavia* is apparently quite restricted, while, on the other hand, the introgression between *A. glabra* and *A. octandra* is widespread. Where the barriers to crossing are slight, an increased variability in the participating populations is brought about by the segregation and independent assortment of the various genes and alleles. Although the influence is mainly on one of the parents, reciprocal introgression does occur in all cases in varying degrees.

The significant point is that even with such a great amount of gene flow into certain species (e. g., *A. sylvatica*), they remain distinct. Heiser (1949), in discussing such species, states that "perhaps the ability to remain distinct in spite of hybridization entitles them rightfully to the designation of 'species'." The apparent discontinuity in breeding, which keeps these entities

apart, is, in my opinion, a very important criterion for the recognition of the species in *Aesculus* section *Pavia*.

It is thought that introgression in section *Pavia* has been going on during relatively recent times only. Presumably these species arose by allopatric speciation possibly in the Appalachians, and evolved independently for some time, but without developing complete barriers to interbreeding. During or after Pleistocene the species ranges came together—because of expanding ranges and/or migrations of the populations. Once sympatric, introgression could proceed.

Introgression may be of primary importance as a factor in the future evolution of the eastern buckeyes. With continued gene flow and heightened variability within the populations, there is an increased plasticity of the species—a plasticity which may make for increased survival value in the face of changing environmental conditions.

In connection with the analysis of hybridization in *Aesculus*, the cytology, or more specifically the karyology, of the genus was studied. Although cytological studies are rather monotonous in this genus, the study of chromosomes—number and morphology plus their meiotic behavior—does, to some extent, aid in indicating hybridization between species.

Very little cytological investigation was undertaken during the course of this study, but the chromosome number ( $n = 20$ ) was checked in many specimens representing six of the species. It was hoped that chromosome counts of *A. parryi*, *A. californica* and *Billia* spp. could be made, but this was not accomplished because of the lack of adequate living material. No published counts have been found for the above or for *A. indica*, *A. assamica* or *A. turbinata*. A tentative count was made from root tips and anthers of *A. californica*, but in each case the count of  $2n = 40$  and  $n = 20$  was somewhat subjective. The numbers in all other species as well as in many of the described hybrids and, now unrecognized, varieties and species, have been reported by one or more authors (Darlington and Wylie, 1956; Gaiser, 1930, 1930a; Seitz, 1951; Wang, 1939).

The only reported differences in the chromosome number in the family are for *A. carnea* and *A. plantierensis*, which have been mentioned earlier. According to Upcott (1936), secondary



pairing and the occasional formation of quadrivalents, suggests that possibly the parents are tetraploids and therefore *A. carnea* is actually an octoploid and *A. plantierensis* a hexaploid. Stebbins (1950) refers to this by using *Aesculus* as one of the examples of a genus in temperate regions of which the base number ( $x = 20$ ) is probably of ancient polyploid derivation.

Individual chromosomes of a karyotype in *Aesculus* do not vary markedly in shape or size (Hoar, 1927); there are, however, slight differences in the chromosome size of different species. Skovsted (1929) found a recognizable difference in size between *A. hippocastanum*, *A. glabra* and *A. parviflora*, all of which have relatively small chromosomes, and *A. pavia* and *A. octandra*, which have larger ones.

Probably the most significant evidence to come from cytological investigations of *Aesculus* has been the recognition of meiotic irregularities. These are discussed particularly by Hoar (1927) and to some extent by Pelletier (1935). Hoar recognized no irregularities in the "good" species, but in others, lagging chromosomes and polyspory were common, and the percentages of abortive pollen were high. He found that such irregularities in meiosis and pollen formation were common in both artificial and natural hybrids. He therefore concluded that such irregularities found in *Aesculus* specimens placed "their ancestry under suspicion." I have checked the frequencies of abortive pollen in numerous specimens. Those recognized by floral characters as being of hybrid origin have high percentages of abortive pollen, and those identified as "good species" have all viable pollen or only a very low percentage of abortives. This agrees entirely with the present concepts of the species, and is additional evidence for introgression between species in the section *Pavia*.

Hoar (1927) raised one interesting question concerning the propagation of the plants with high percentages of abortive pollen. Some are clonal, propagated to some extent by root sprouts, but there is no indication of apomictic seed production in any of the species. Obviously, there is enough viable pollen to result in a number of seeds each season. A perennial plant such as the buckeye is not dependent on a great quantity of seeds each season for survival. The great number of abortive pollen grains, however, could result in an incomplete fertilization,

which has been suggested earlier (Hardin, 1955) as a possible cause for the relatively few seeds which are produced per capsule.

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## LITERATURE CITED

- ANDERSON, EDGAR. 1949. *Introgressive Hybridization*. John Wiley & Sons, Inc., New York.
- . 1953. *Introgressive Hybridization*. *Biol. Rev.* **28**: 280–307.
- DARLINGTON, C. D., AND A. P. WYLIE. 1956. *Chromosome Atlas of Flowering Plants*. Second Edition. The Macmillan Co., New York.
- GAISER, L. O. 1930. Chromosome numbers in Angiosperms, II. *Bibliographia Genetica* **6**: 171–466.
- . 1930a. Chromosome numbers in Angiosperms, III. *Genetica* **12**: 161–260.
- HARDIN, JAMES W. 1955. Studies in the Hippocastanaceae, I. Variation within the mature fruit of *Aesculus*. *RHODORA* **57**: 37–42.
- . 1957. Studies in the Hippocastanaceae, III. A hybrid swarm in the buckeyes. *RHODORA* **59**: 45–51.
- HEISER, CHARLES B., JR. 1949. Natural hybridization with particular reference to introgression. *Bot. Rev.* **15**: 645–687.
- HOAR, C. S. 1927. Chromosome studies in *Aesculus*. *Bot. Gaz.* **84**: 156–170.
- JOHNSON, L. P. V. 1939. A descriptive list of natural and artificial interspecific hybrids in North American forest-tree genera. *Canadian Jour. Research, Sect. C—Bot. Sci.* **17** (12): 411–444.
- LOUDON, JOHN C. 1869. *An Encyclopaedia of Trees and Shrubs*. pp. 123–134. Frederick Warne & Co., London.
- PELLETIER, MARCEL. 1935. Recherches cytologiques sur l'*Aesculus Hippocastanum* L. *Le Botaniste* **27**: 279–322.
- SARGENT, C. S. 1913. *Trees and Shrubs*. Vol. 2, pp. 257–270.
- SEITZ, FRIEDRICH WILHELM. 1951. Chromosomenzahlenverhältnisse bei Holzpflanzen. *Zeitschrift für Forstgenetik und Forstpflanzenzüchtung* **1** (1): 22–32.
- SKOVSTED, AAGE. 1929. Cytological Investigations of the genus *Aesculus* L. *Hereditas* **12**: 64–70.
- STEBBINS, G. LEDYARD. 1950. *Variation and Evolution in Plants*. Columbia University Press, New York.
- SVENSON, H. K. 1941. Notes on Tennessee Flora. *Jour. Tenn. Acad. Sci.* **16**: 111–160.
- UPCOTT, MARGARET. 1936. The parents and progeny of *Aesculus carnea*. *Jour. Genetics* **33**: 135–149.
- WAGNER, W. H., JR. 1954. Reticulate evolution in the Appalachian Aspleniums. *Evolution* **8**: 103–118.
- . 1956. A natural hybrid, *Adiantum* × *tracyi* C. C. Hall. *Madroño* **13**: 195–205.

- , AND D. J. HAGENAH. 1954. A natural hybrid of *Polystichum lonchitis* and *P. acrostichoides* from the Bruce Peninsula. *RHODORA* **56**: 1–6.
- WANG, D. T. 1939. Karyokinetic study on *Aesculus chinensis* Bunge. *Bull. Fan Mem. Inst. Biol., Bot. ser.* **9** (3): 195–201.

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A REVISION OF THE VERNAL SPECIES OF  
HELENIMUM (COMPOSITAE)

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(continued from p. 178)

To complete the confusion, since 1874 both *Galardia fimbriata* Michx. and *Leptopoda fimbriata* T. & G. have often been considered to be the same taxon, despite the inadequate understanding of either the nomenclatural or taxonomic complexities surrounding both of the binomials. This has led to a confused application of both Wood's *H. fimbriatum* and Gray's *H. fimbriatum* to various taxa to be found from the Carolinas to Texas. Moreover, the parenthetical author has been variously cited as either Michaux or Torrey and Gray or else left out completely. Nevertheless, the taxon described by Torrey and Gray as *Leptopoda fimbriata* is recognized here as a distinct species and that this species is not the same as either of the two elements (*H. vernale* and *H. pinnatifidum*) included within *Galardia fimbriata* Michx.

There appears, then, to be only one course of action possible under the provisions of the rules and preamble of the present Code. This course of action is to invoke the application of Article 65 by which an ambiguous name must be rejected. Therefore the name *Helenium fimbriatum* is hereby rejected from use for this species. In order to avoid further confusion and inasmuch as Thomas Drummond was the first person to collect this plant, the epithet *Drummondii* has been chosen to form the new name *Helenium Drummondii* for this species.

*Helenium Drummondii* is most likely to be confused, upon superficial examination, with *Helenium vernale*. The character of the pappus, however, is sufficient to result in a ready separation of the two. In *H. Drummondii* it is usually longer and always distinctively slashed into a multitude of *fimbriae*, the *fimbriae*